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THE COMPARATIVE MORPHOLOGY OF THE FUNGI

BY JAMES ELLIS HUMPHREY.

UNTIL a very recent date the whole history of the truly morphological study of the fungi might have been epitomized in the mention of two names,—Tulasne and DeBary. Beginning with the earlier publications of the brothers Tulasne, which culminated in their monumental "Selecta Fungorum Carpologia," and continued in the "Beiträge zur Morphologie der Pilze" and other works of DeBary and his students, the contributions to our knowledge of the structure of the fungi, their polymorphic fruit forms and their genetic relationships, have increased in number and importance. But the time has come when to the names mentioned must be added a third,—that of a pupil of DeBary, though for a long time not of his "school." It is now nearly twenty years since there appeared the first of a series of quarto memoirs, of which the tenth has just been issued, which give their author his conspicuous rank among myco-morphologists. The first six of the series may be regarded as preliminary studies, which contain the early views of their author, and record the dawnings of the broad morphological ideas which are developed in their completeness in the last four numbers. It is the primary purpose of this paper to present in outline to American readers the results and conclusions contained in these last four parts of the "Untersuchungen aus dem Gesammtgebiete der Mykologie"[1] of Prof. Brefeld, of the German Academy at Münster, in Westphalia. The parts named comprise 884 pages of text, with 37 lithographed plates, and their very bulk is perhaps a sufficient excuse for the present abstract; while the importance of their contents and the light which they throw on many heretofore doubtful forms and problems render at least a general knowledge of them of the greatest importance to any one who would keep himself in line with botanical progress. And it may safely be predicted that their influence on the future study of the fungi will be of a most positive and fruitful character.

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[1] Untersuchungen aus dem Gesammtgebiete der Mykologie. Von Dr. Oscar Brefeld, Ord. Professor der Botanik, etc. VII. and VIII. Hefte, Basidiomyceten. Leipzig, 1888-'89. IX. and X. Hefte, Die Hemiasci und die Ascomyceten. Münster, 1891.

Assuming, with all writers on the subject, that the simplest and most primitive fungi, which retain undoubted sexual characters, the Zygomycetes and the Oömycetes, have been derived from the lower Algæ, we find them developing, in common with some of the latter, two types of reproductive organs: sexual organs, which usually produce resting-spores, and non-sexual organs. Of the latter, the sporangium of Mucor may be regarded as the most primitive type. In this we find a roughly globular sac of very variable size, raised upon a stalk, from whose contents (originally undifferentiated protoplasm) have been formed, at maturity, a large number of rounded spores, varying considerably in size and determined, as to their number, by their own size and that of the sporangium in which they were formed. The closely related genus Thamnidium[2] bears similar sporangia at the apices of erect hyphæ, and others of a second sort on lateral branches. These latter, known as sporangiola, are essentially only miniature sporangia, in which the number of spores has become reduced to four, or even two. In one species of Thamnidium the terminal sporangium is often aborted, leaving only the the sporangiolia; and the relative abundance of the two forms can be largely controlled by varying the conditions of the culture. From this condition of things it is an easy step to that in which the terminal sporangium is habitually suppressed, and the contents of the sporangiole have been reduced to a single spore. This condition is realized in Chætocladium, whose reproductive organs are no longer sporangiola which set free their spores by rupturing, but "closed sporangia" or conidia. A comparison of the two species of Chætocladium shows the last stage in the reduction. In *C. fresenianum* the conidium begins its germination by throwing off its outer coat, a process morphologically equivalent to the rupture of the sporangium-wall; but no such preliminary process occurs in *C. jonesii*, in which is thus reached the full character of the conidium.

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[2] The forms referred to in the following pages will nearly all be found described, and many figured, in the English translation of DeBary's "Comparative Morphology of the Fungi," published by Macmillan & Co.

Brefeld here adopts the familiar name previously applied to certain non-sexual spores, and extends to some extent, while in other directions limiting, its application, and gives it a definite morphological value. The conidium, then, may be defined as a reproductive organ, morphologically equivalent to the sporangium, and derived from it by reduction; or as a one-spored, closed sporangium. As the author well says, we have here a theoretically ideal series of stages, complete at every point. A similar set of steps leading from the sporangium to the conidium can be traced among the Oömycetous forms, although less complete and less convincing.

Not only does the development of the conidia-bearing threads or conidiophores vary widely in different species, but within the limits of species it may be greatly modified by external conditions. The study of the structure and development of a very large series of forms of Basidiomycetes has shown that in some instances the true basidia characteristic of these fungi are accompanied or preceded by conidiophores which under certain conditions assume a form practically indistinguishable from the basidia; and the facts brought out lead irresistibly to the conclusion that the *basidium*, with its sterigmata and spores, must be regarded as a definite and unvarying conidiophore. Two species which show this relation very clearly are *Pilacre petersii*, which, formerly of doubtful relationship, is here shown to represent a special type of primitive Basidiomycete, and that which the author calls *Heterobasidion annosum* (= *Polyporus annosus* Fr., *Trametes radiciperda* Hartig).

The basidia of the various Basidiomycetes are not of a single type, and cannot be referred to a common origin. Those of the simplest of the group are divided by cell-walls into several (usually four) parts, each of which gives rise to a sterigma and spore. And here we find two forms: basidia of elongated form, with transverse divisions, characteristic of Pilacre and Auricularia and of the Uredineæ; and basidia of rounded form, divided by walls parallel to their longer axes, occurring in the Tremellineæ, which group is considerably reduced in size by this new limitation. The fungi comprised under the groups above mentioned constitute Brefeld's Protobasidiomycetes, in distinction to his Autobasidiomycetes, which form the main bulk of the order, and have undivided basidia. Nearly all of these latter have basidia of the familiar short form, with terminal sterigmata and spores; but in the genus Tulostoma the spores are borne laterally, and the basidia resemble those of Auricularia, without their divisions.

The important point to be noted here is that the basidium furnishes the essential character of the Basidiomycetes, as was long ago recognized by DeBary in the very appropriate name of the group, although on much less substantial morphological grounds; that the basidium is more fundamental than any form of fruit body, and that the very various fruit forms have grown up within the group after differentiation of the types of basidia from their ancestral conidial forms. This subsequent development of the fruit body has produced results so striking and has followed such similar lines in the two great groups of fungi—the Basidiomycetes and the Ascomycetes—that the tendency has been to emphasize the differences thus brought about, with the result that we have lost sight of the primitive character of the basidium and the ascus.

Among the Protobasidiomycetes we find in Pilacre a fruit form of angiocarpous structure, while the other forms are strictly gymnocarpous. Of the Autobasidiomycetes, the simplest gymnocarpous forms comprise the gelatinous Dacryomyceteæ, formerly included in the Tremellineæ; the Tomentelleæ, separated from the Thelephoreæ; and the Clavarieæ. The basidium of the first-named family is somewhat pitchfork-shaped, with two large sterigmata; but in the others we meet with the typical club-shaped basidium, with small, spine-like sterigmata. In the Tomentelleæ we have clearly the primitive Autobasidiomycetes, consisting of very loose wefts of hyphæ, upon which are borne, irregularly and indiscriminately, the basidia, which arise precisely as do the conidiophores of many other fungi. These pass into the definite fruit bodies with more or less restricted hymenial surface of the Clavarieæ and of the hemiangiocarpous families, he Thelephoreæ, Hydneæ, Polyporeæ, and Agaricineæ. Following these must be placed the angiocarpous forms, usually known under the name of Gasteromycetes. The author suggests that these last may have been derived either from the gymnocarpous forms through the hemiangiocarpous ones, or from the Protobasidiomycetes through forms like Tulostoma. It is worthy of note that development along parallel lines in the two great groups of fungi, in consequence of the acquirement of a subterranean mode of life, should have brought about such striking similarity as is presented in the fruit bodies of the Tuberaceæ and the Hymenogastreæ.

The culture of a large number of Basidiomycetes has brought to light much that is new concerning their life-histories, and emphasizes the fact that polymorphism is by no means a characteristic of the Ascomycetes alone, or even chiefly of that group, as has been thought since the Tulasnes' classic researches. Brefeld shows that in this respect there is little to choose between the two groups. Since the basidium is merely a modified conidiophore, it might be expected that the Basidiomycetes would produce, as accessory fruit forms, unmodified and still indefinite conidiophores. And such is found to be the case with a number of forms, some of which have been already mentioned. In some Tremellineæ, Polyporeæ, and other forms, conidia have been for some time known. Another accessory fruit form which is always morphologically of strictly secondary value, although it often becomes of primary importance histologically, is the chlamydospore. These occur very frequently in cultures of Basidiomycetes, and in their simplest and commonest form are short joints cut off from the fungus threads, occurring in chains and constituting members of the old form-genus Oidium. They may often reproduce themselves indefinitely under suitable conditions without a hint of their true relationships; as in the case with the form known as *Oidium lactis*. Much less common are the more highly differentiated chlamydospores formed, like the Oidia, from joints of the mycelium, which occur in Nyctalis, Oligoporus, Fistulina, etc. These forms may be restricted to special parts of the fruit body, as to the hymenium in *Nyctalis parasitica*, or to the top of the pileus in *N. astrophora*. The species of Brefeld's new genus, Oligoporus, have special chlamydosporic fruits distinct from their hymenial fruit body, which have been long known under the generic name Ptychogaster or Ceriomyces. In cultures of some species, notably in the case of *Fistulina hepatica*, branching aërial hyphæ produce clusters of chlamydospores almost indistinguishable from conidiophores with conidia. And in nature it becomes sometimes practically impossible to say whether a given accessory fruit form is morphologically conidial or chlamydosporic. In *Mucor racemosus* and allied forms, in which this secondary fruit form is typically present, and which Brefeld proposes to separate under the generic name Chlamydomucor, it may readily be seen that Oidia and true chlamydospores represent modifications of the same form. The chlamydospore, then, is morphologically independent of and secondary to other fruit forms, although it frequently becomes the physiological equivalent of any, and may largely suppress and replace others by being introduced into the primary cycle at any stage in the development of the fungus.

The Uredineæ have been mentioned above among the families of Protobasidiomycetes which have transversely divided basidia and lateral spores. This view of the so-called "promycelium" and "sporidia" which are developed at the germination of the "teleutospores" is an old one, which has been gaining ground in recent years, and is now emphasized by Brefeld as the most tenable and philosophical one. The three spore forms, æcidiospores, uredospores, and teleutospores, are regarded as different forms of chlamydospores, which reach their highest development in this group, and, in the teleutosporic stages of Gymnosporangium and Cronartium, look toward the differentiation of a fruit body and connect with the Auricularieæ. It is pointed out that various Autobasidiomycetes produce both Oidia and true chlamydospores, and that the intermediate sterile cells found between the latter occur also in the spore-chains of Cæoma. While the germination of the other forms is purely vegetative, the teleutospore gives rise to a basidium which is typically four-spored, the one-spored condition in Coleosporium being paralleled by that in Kneiffia of the Hydneæ. Our author believes that in this fructificative germination lies the true character of the chlamydospore, which has been lost in other groups, leaving it as the essential feature of the Uredineæ and the related Ustilagineæ. No species which has teleutospores can be considered " incomplete," the only such species being those whose teleutospores, and therefore whose basidia, are unknown. A single other fruit form is common among the Uredineæ, the so-called " spermogonium," but its relations may better be discussed in connection with those of the similar structures which occur abundantly among the Ascomycetes.

The Ustilagineæ have been a source of much perplexity as to their relationships, although the similarity of the spore-germination in many forms to that of the Uredineæ has indicated the propriety of placing these groups near together in the system. In their formation the spores of this group closely resemble those of Ptychogaster and other chlamydospores. In germination many of them produce structures which strikingly recall the basidia and spores of the Uredineæ, and a few produce merely vegetative filaments, perhaps by degeneration from the former type; while those of a large group of forms give rise to undivided filaments, each with a whorl of conidia at its apex, representing clearly the basidia of the Autobasidiomycetes. In the great majority of these fungi the chlamydospores are the only fruit form developed, but some of them produce also conidiophores with typical conidia.

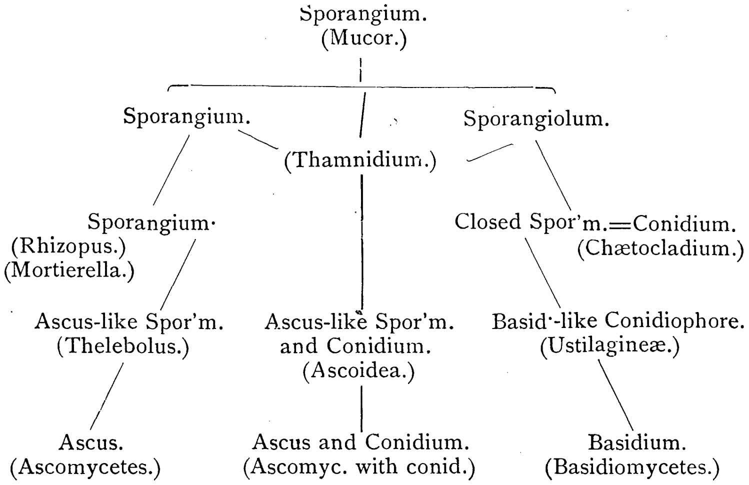
The basidia of the Ustilagineæ are distinctly more primitive than those of any of the true Basidiomycetes, in that they are much more variable in form, size, and number of spores, in all those particulars,—that is, whose definiteness constitutes the true basidium. Brefeld therefore places the group, under the name of Hemibasidii, between the Phycomycetes and the true Basidiomycetes, as a connecting link; and divides it on the basis of the two types of basidia already described, into Protohemibasidii and Autohemibasidii, corresponding to the two groups of Basidiomycetes. These two groups coincide with the two families into which the smuts have been divided by Schroeter on the basis of spore-germination, the Ustilaginei and Tilletiacei.

Passing now to the other great group of fungi, we find it also especially characterized by a particular form of reproductive organ, the *ascus*, which has given to the order its name, Ascomycetes. This name has, however, been used in a rather more restricted sense than that of Brefeld. This is due to the fact that the characteristic of the group has been considered to be the ascus fruit, and not the ascus itself. But here, as in the Basidiomycetes, the fruit body is a secondary development within the group, subsequent to, or at most contemporary with, the differentiation of the ascus. Morphologically, the ascus is to be regarded as a reduced and definite sporangium whose form is constant, at least within the limits of the species, and whose spores, typically eight, are in most cases definite and constant in number. Intermediate conditions between the indefinite and definite extremes are distinctly to be recognized. The numerous and striking subdivisions which occur in the spores of the Ascomycetes, so useful systematically that they form the basis of Saccardo's carpologic system, are regarded by our author as germination phenomena, analogous to those seen in Dacryomyces and the Tremellineæ, which have become pushed forward into the earlier stages of spore development.

From the great body of the Ascomycetes which have a well-developed fruit body, and are called by him Carpoasci (constituting the whole of the order, according to the limitations of DeBary), Brefeld separates the forms included under Endomyces, Taphrina and Exoascus, and Ascocorticium nov. gen., as Exoasci. The members of this group, corresponding to the Tomentelleæ among the Basidiomycetes, have their asci produced, free and naked, directly from the mycelium. The Carpoasci include angiocarpous forms, the Gymnoasci, Perisporiaceæ (including Tuberaceæ), and the Pyrenomycetes; and hemiangiocarpous forms, grouped under the Hysteriaceæ and the Discomycetes. One family of the latter, the Helvellaceæ, may yet prove to deserve separation from that group. The early stages of its members are unknown, but they may be found to be truly gymnocarpous.

If we go back once more to the sporangium of Mucor, we may trace a very instructive series up to the ascus fruit of the Carpoasci. In Rhizopus we have a plant which differs from Mucor essentially in producing from a given region several threads, some of which bear sporangia like those of Mucor (fertile threads), while others become rhizoidal (sterile threads). In Mortierella these sterile threads become woven together to form a dense capsule about the base of the fertile ones, which are long and stout. It is easy now to suppose the fertile threads reduced in length until the sporangia at their ends are withdrawn within the capsule, and just this condition is found in *Thelebolus stercoreus*, whose fruit body contains a single many-spored sporangium. From this condition a further step leads to that so familiar in the genera Sphærotheca and Podosphæra, in which the indefinite sporangium of Thelebolus has become a well-defined ascus, while the capsule is essentially unchanged. The simplest of the Carpoasci are the Gymnoasci, which have a well-marked ascus, but whose capsule consists of very loosely entangled hyphæ. Another line may be traced from some Choanephora-like form, with sporangia and conidia, through the new plant described as *Ascoidea rubescens*, which produces ascus-like sporangia and conidia, to the numerous conidia-bearing Ascomycetes.

Having seen how all of the primary fruit forms of the higher fungi, the ascus, the conidium, and the basidium, are derivable from the simple sporangium of the Phycomycetes, we may summarize the whole graphically as follows:



In the study of more than 400 Ascomycetes there has been found the greatest diversity in the time of the appearance of the ascus in the fruit body, and in its relations to the tissue of threads composing that body. In some cases the asci and the intermingled sterile threads, or paraphyses, arise as branches of the same hyphæ; or, again, the two may rise from separate hyphal systems which are differentiated early and remain structurally distinct. This distinction is never seen in the Basidiomycetes and is not to be expected, since none of their ancestral Phycomycetous forms show any such differentiation as has been described in Rhizopus and Mortierella, which are believed to represent ancestral forms of the Ascomycetes. Brefeld points out that it is this differentiation of fertile and sterile threads which has given rise to the doctrine of the sexuality of the Ascomycetes of which DeBary has been the especial champion. He contends elaborately and with the strongest emphasis that there exists no proof whatever that the so-called "ascogonium" and "pollinodium" observed in certain Carpoasci are of any sexual significance. This view, he maintains, has been reached deductively, and not inductively;[1] by inference, and not by proof. The analogy of the sexual organs of the Florideæ has exerted a strong influence on the interpretation of the significance of the structures in question and of the so-called "spermatia," to be discussed later; yet the Florideæ and the Ascomycetes are as little related as any two groups of Thallophytes. The fusion of the initial fertile filament with one or more of the surrounding sterile filaments has no more significanc than any of the hyphal fusions, so common among fungi. It is quite as reasonable to suppose that, in the great number of forms in which this early differentiation is not observed, it has become obscured or lost in the bewildering tangle of hyphæ, as that typically sexual fungi have lost their sexual organs by abortion.

Two fungi, Thelebolus and Ascoidea, have been mentioned as having ascus-like sporangia, and as holding an intermediate place between the Phycomycetes and the true Ascomycetes. With these should be mentioned a third genus, Protomyces. This genus has been recognized as related to the Ustilagineæ, since its spores are developed from the hyphæ in much the same manner as those of the latter group, although they germinate differently. Like those of the Ustilagineæ, its spores, as ordinarily observed, must be regarded as chlamydospores, and, like most of those, their germination is fructificative; but the product of germination is a sporangium which shows a tendency towards the more definite form of the ascus. In this view Brefeld adopts the early explanation of DeBary, the first student of the genus, which was afterwards reconsidered by him. These three intermediate forms hold the same relations to the Ascomycetes as do the Ustilagineæ to the Basidiomycetes, and similarly they are grouped together under the name Hemiasci; Ascoidea and Protomyces, with naked sporangia, constitute the Exohemiasci; and Thelebolus, with its well-developed fruit body, is the type of the Carpohemiasci. These two intermediate groups, the Hemiasci and the Hemibasidii, are made to constitute, under the name Mesomycetes, one of the three great divisions of the fungi, coördinate with the Phycomycetes and the Mycomycetes. This last group includes the true Basidiomycetes and Ascomycetes, the "higher fungi."

Of the accessory fruit forms, chlamydospores are not common among the Ascomycetes, though both Oidia and the typical form may occur. Unquestionable specimens of the latter are known in the Sepedonium and Mycogone stages of those parasites of "toadstools" and similar fungi which belong to the genus Hypomyces. While, theoretically, there is no reason why unmodified sporangia or conidiophores modified into basidia should not occur as accessory forms in the Ascomycetes, they have, in fact, never been observed; but the ordinary conidiophores are very abundant,—much more so than in the Basidiomycetes. These may arise from retrograde development of sporangia still left after the differentiation of the asci; or they may represent the conidia of Choanephora-like forms whose sporangia have become asci. They are formed either by budding from the ascospores at germination, after or even before their escape from the ascus; by abstriction from the germ-tube directly; or on distinct conidiophores. The budding of conidia from the ascospore recalls the similar cases among the lower Basidiomycetes; but it may be forced a step farther back and take place within the ascus, giving to it an indefinitely polysporic appearance. Conidia of this type usually increase freely by yeast-like budding, like those of the Ustilagineæ; and, excepting those of the Taphrinæ, they usually develop readily, under suitable conditions, into filaments. The less specialized conidiophores have their conidia scattered over their entire length, and a gradual advance may be traced from this form to those whose conidia are wholly restricted to their tips.

Besides occurring separately, conidiophores are found grouped into dense clusters, such as have been described under the name Coremium, or into more extensive, compact "stromata." In simpler cases the surfaces of these stromata are flat; but they may be ridged or folded, and a fold may increase in depth until its edges meet, and a closed cavity is the result. Such a series may be traced in Nectria and its allied genera of the Hypocreaceæ. Closed conidial fruits which may be supposed to have originated in this way are very common among the Ascomycetes, and have long been known under the name *pycnidia*. They are known among the Basidiomycetes only in the Uredineæ and the new Tremellaceous genus Craterocella. In their development pycnidia present two types. They originate by the interweaving of previously formed threads (symphyogenic), or by the fusion of newly formed threads into a parenchymatous mass (meristogenic). Within the cavity of the pycnidium spores may be formed from all the cells or only from the terminal cells of the spore threads, just as in the case of free conidiophores. Two distinct forms of conidia may be borne on the same conidiophore or within the same pycnidium; or they may be separated, and so lead to distinct conidial or pycnidial forms on the same plant.

A fruit form very common among the Ascomycetes and the Uredineæ is that which has been known as the *spermogonium*, on account of its supposed sexual nature. This organ is structurally like the pycnidium; but the spore-like bodies developed in its cavity have been supposed, chiefly from the analogy of the spermatia of the Florideæ, on account of their minute size and the fact that they had never been seen to germinate, to be male sexual elements. But Brefeld and his pupil, Möller, have succeeded not only in observing the germination of these bodies, but in raising from them fertile mycelia, thus clearly proving them to be a form of pycnidial conidia with somewhat weakened or reduced germinative power. Thus falls another supposed support of the sexual theory of the Ascomycetes.

The conditions governing the development of the Ascomycetes are very little known. The ascus usually closes the cycle of development as the most perfect and most highly differentiated fruit form. In artificial cultures of fungi of this order it is usually found that conidial and pycnidial spores yield the fruit form which produced them, and rarely give rise to the ascus-fruit.

From what has been said above, it will be seen that all the more specialized fungi are considered to be descendants of forms identical with, or similar to, living Phycomycetous species, and to have retained none of their sexual characters, since all their primary fruit forms have been derived from, and are referable back to, the Zygomycetous sporangium. We may summarize the points brought out and the relationships indicated by means of the following tabular view :

A. PHYCOMYCETES.

I. ZYGOMYCETES.				II. OÖMYCETES.	
Exosporeæ.			*Carposporeæ.*		
With Sporan.	With Sporang. and Conid.	With Conidia.		With Sporang. or Conidia.	With Conidia.
Mucor.	Choanephora.	Chætocladium.	Rhizopus.	Peronosporeæ.	Entomophthoreæ.
Thamnidium.		Piptocephalis.	Mortierella.	Saprolegnieæ.	
				Chytridieæ.	

B. MESOMYCETES.

III. HEMIASCI.			IV. HEMIBASIDII.	
Exohemiasci.		*Carpohemiasci.*	*Protohemibasidii.*	*Autohemibasidii.*
Ascoidea.	Protomyces.	Thelebolus.	Ustilagineæ.	Tilletieæ.

C. MYCOMYCETES.

V. ASCOMYCETES.			VI. BASIDIOMYCETES.				
Exoasci.	*Carpoasci.*		*Protobasidiomycetes.*		*Autobasidiomycetes.*		
	Angiocarpous.	Hemiangiocarpous.	Gymnocarpous.	Angiocarpous.	Angiocarpous.	Gymnocarpous.	Hemiangiocarpous.
Endomyces.	Gymnoasceæ.	Hysterieæ.	Uredineæ.	Pilacreæ.	Lycoperdaceæ.	Dacryomyceteæ.	Thelephoreæ.
Taphrina.	Perisporieæ.	Discomycetes.	Auricularieæ.		Nidularieæ.	Clavarieæ.	Hydneæ.
Ascocorticium.	Pyrenomycetes.		Tremellineæ.		Phalloideæ.	Tomentelleæ.	Polyporeæ.
					Hymenogastreæ.		Agaricineæ.

Such in outline are the results to which Prof. Brefeld has been led by the long and careful study of a remarkably large number of fungi of all groups and in all stages, with the assistance of the most elaborate and precise culture methods yet devised. In all his work he has had the help of trained assistants, and in that on Ascomycetes has had also the collaboration of Dr. Franz von Tavel, of Berne, whose previous researches on the development of the Pyrenomycetes are well known. One need not accept these conclusions in all their details in order to recognize the fact that they are the result of the application of a keen morphological insight to a much wider and fuller series of observations than has been at the command of any previous writer. We may regret that the author finds it necessary to introduce so much of a personal and polemic nature into some of his discussions, especially that concerning the sexuality of the Ascomycetes, or to treat so unceremoniously his former master, DeBary, and others of that school who have antagonized and criticised his views; yet it must be remembered that the provocation has sometimes been very great.

But, after all is said, we have in this characteristic work of a remarkable man a series of memoirs which must always remain classic and a prime authority for the student of the morphology of the fungi, both as the record of a great number of new facts, and as the first statement of a new and consistent comparative morphology.

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